THE PEABODY MUSEUM OF NATURAL HISTORY
BULLETIN 2

THE OSTEOLOGY OF *EPOREODON SOCIALIS* MARSH

BY

MALCOLM RUTHERFORD THORPE, PH.D.

NEW HAVEN
THE PEABODY MUSEUM OF NATURAL HISTORY
YALE UNIVERSITY
1931

PEABODY MUSEUM OF NATURAL HISTORY

TRUSTEES

James Rowland Angell, Ph.D., Litt.D., LL.D.
Alfred Lawrence Ripley, M.A.
John Villiers Farwell, M.A.
Edwin Musser Herr, Sc.D.
Clarence Blakeslee, M.A.
Rev. William Adams Brown, Ph.D., D.D.

DIRECTOR

Richard Swann Lull, Ph.D., Sc.D.

CURATORS

Edward Salisbury Dana, Ph.D., Curator of Mineralogy, Emeritus.
Charles Schuchert, LL.D., Sc.D., Curator of Invertebrate Paleontology, Emeritus.
Stanley Crittenden Ball, Ph.D., Curator of Zoology.
Carl Owen Dunbar, Ph.D., Curator of Invertebrate Paleontology.
William Ebenezer Ford, Ph.D., Curator of Mineralogy.
George Grant MacCurdy, Ph.D., Curator of Anthropology.
Cornelius Berrien Osgood, Ph.D., Assistant Curator of Anthropology.
Albert Eide Parr, M.A., Curator of the Bingham Oceanographic Collection.
Malcolm Rutherford Thorpe, Ph.D., Curator of Vertebrate Paleontology.

DOCENTS

Dorothy Emma Arnold, B.A.
Gertrude Hotchkiss Clark.
Mildred Cynthia Beulah Porter, M.A.

RESEARCH ASSOCIATES

George Grant MacCurdy, Ph.D., Research Associate in Prehistoric Archæology.
Malcolm Rutherford Thorpe, Ph.D., Research Associate in Vertebrate Paleontology.

THE PEABODY MUSEUM OF NATURAL HISTORY
BULLETIN 2

THE OSTEOLOGY OF *EPOREODON SOCIALIS* MARSH

BY
MALCOLM RUTHERFORD THORPE, PH.D.

NEW HAVEN
THE PEABODY MUSEUM OF NATURAL HISTORY
YALE UNIVERSITY
1931

CONTENTS

INTRODUCTION AND SUMMARY

PROFESSOR Marsh[1] established the genus *Eporeodon* in March, 1875, upon the presence in the skull of prominent auditory bullæ, a larger bodily size, and characteristic of a higher geologic horizon, as distinguished from *Merycoidodon.* He could have used the loss of the pollex on the manus and the total absence of the foramen rotundum in the skull as additional distinguishing characters.

Of the thirteen species of *Eporeodon* already described, two were erected by Professor Marsh, the type specimens of each being in the Peabody Museum of Natural History at Yale University. These species are *E. occidentalis* (the genotype) and *E. socialis.*

Except for occasional references by the author in earlier papers, no description of *E. socialis* has been written, and it is now proposed to describe in detail the various skeletal elements of this form. Professor Marsh figured the superior view of the skull, with the brain in position and the fore and hind feet, in 1884, and the feet again in 1885, but with no text description in either instance.

The cotypes on which *E. socialis* Marsh is founded were collected for Professor Marsh on August 17, 1874, at Scotts Bluff, Nebraska, by M. H. Clifford and A. S. Shelley. The two skeletons lay side by side, the skulls being three inches apart and the vertebral columns nearly parallel. These and other specimens collected at that locality were transported overland to Julesburg, Colorado, and from thence to North Platte, the nearest railway shipping point at that time. These two cotypes are numbered 13118 and 13119, Y.P.M., and the latter was mounted a few years ago.

Cat. No. 13118 is about one-third smaller; the leg bones are slightly smaller and shorter, and the length of each individual vertebral centrum is less than those of the other skeleton. The

[1] Marsh, O. C. Am. Jour. Sci. (3), vol. IX, 1875, p. 249.

skulls show almost no differences. Both animals were fully adult, and the smaller may have been a female. The bones of both cotypes were enclosed in Brule clay.

The skeletal elements have been compared with those of a specimen of *Sus scrofa*, Cat. No. 01580 Y.P.M., with which *Eporeodon socialis* corresponds very closely, except in the skull and dentition. These Oligocene forms must not be considered as the direct ancestors of the modern Suidæ, for in many respects the Merycoidodontidæ are more like *Tragulus* (chevrotain) than the Suidæ, though in others they resemble the suillines. Therefore, while it was more convenient in the preparation of this paper to compare *Eporeodon* with *Sus*, a form available to all students, it must not be considered that its affinities are necessarily all with the Suidæ.

These eporeodonts were gregarious and roamed the plains and forests in herds. They must have been well able to protect themselves, fighting other animals after the manner of the modern peccaries, which are known to tree animals as large and ferocious as the jaguar. Undoubtedly the eporeodonts drew their sustenance mainly from grasses and roots, as indicated by their selenodont dentition. Their canine teeth in both upper and lower dental batteries were well adapted to cutting, and their almost claw-like distal phalanges could have dug up roots easily. The climate in the late Oligocene, when these animals lived, was equable and warm. Dr. G. R. Wieland personally stated that in his opinion, the climate of Wilmington, Delaware, approximates very closely that of the upper Oligocene period in the Great Plains area.

In connection with this paper I am very appreciative of the friendly criticism of Professor Lull, and I am greatly assisted by Mr. R. Weber's illustrations which admirably show the details of the various skeletal elements.

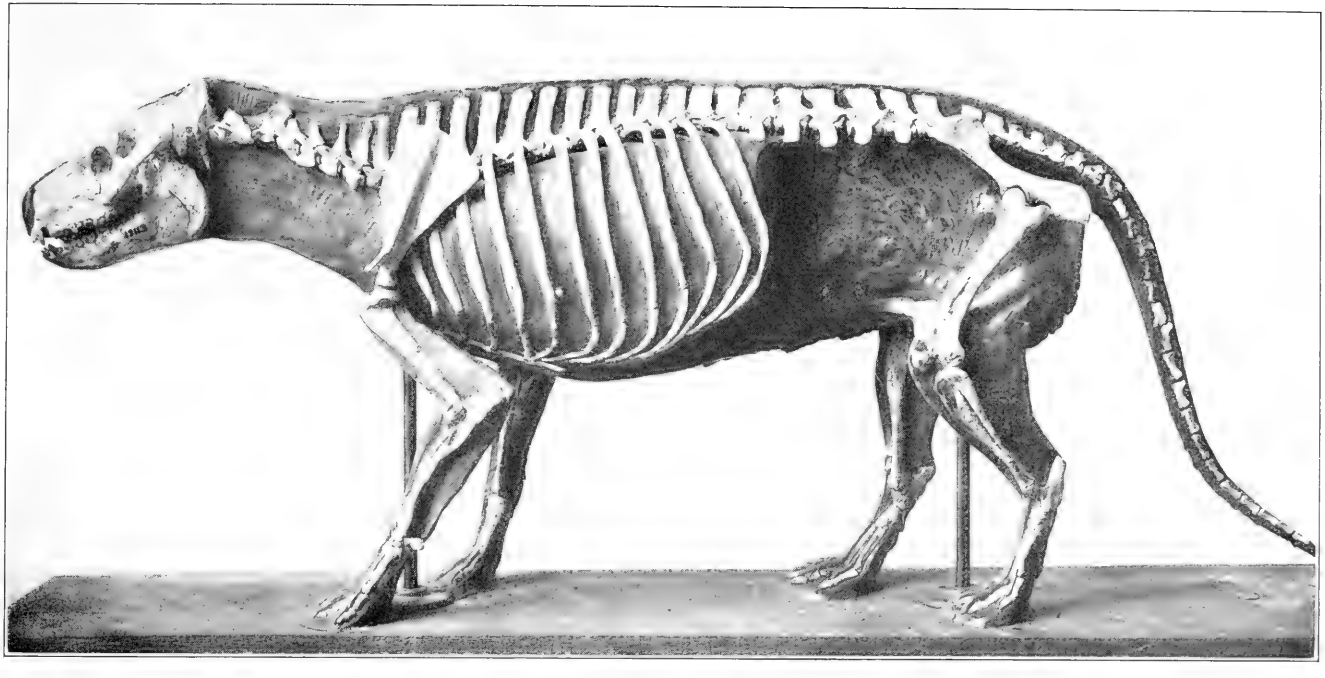


Fig. 1. Mounted skeleton of *Eporeodon socialis* Marsh. Cotype Cat. No. 13119 Y.P.M., with cast of skull of Cotype Cat. No. 13118. (After Thorpe.) $\times\frac{1}{7}$.

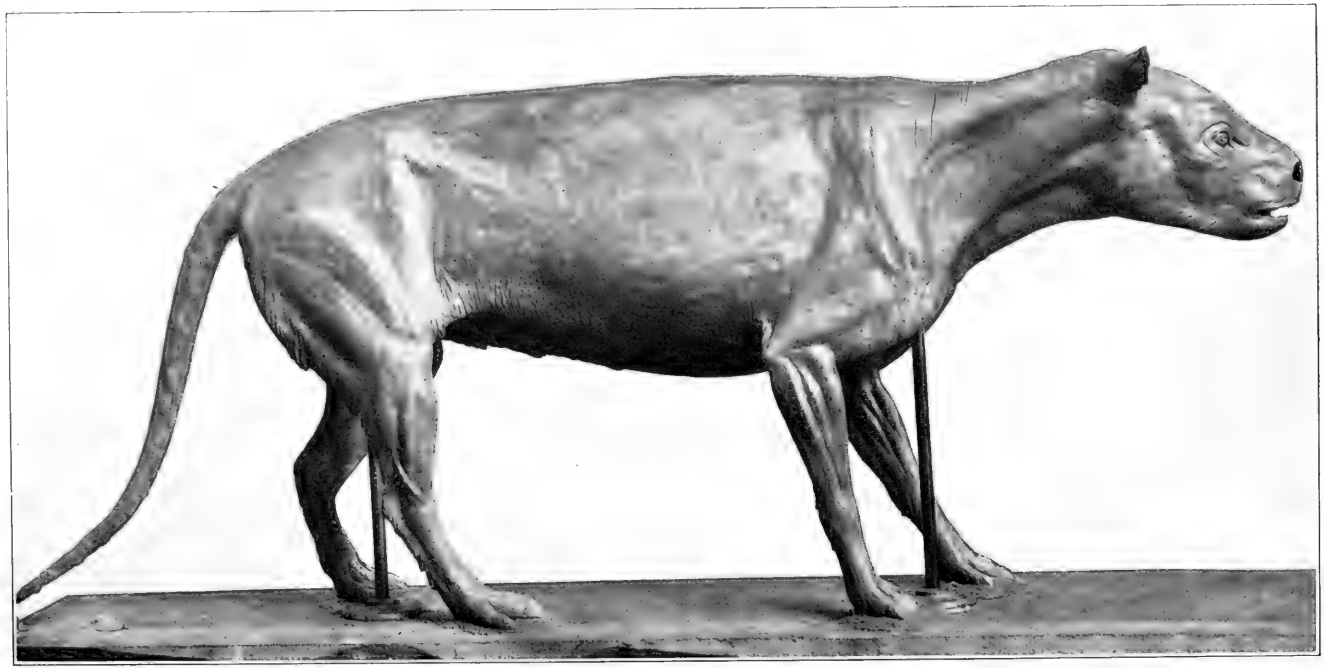


Fig. 2. Flesh restoration of *Eporeodon socialis* Marsh. Reverse of Fig. 1. Cotype. $\times \frac{1}{7}$.

GEOLOGIC HORIZON

THE White River deposits, divided into a lower, the Chadron formation, and an upper, the Brule clay, comprise the strata in the Scotts Bluff area. They are both freshwater deposits. The sandy coarse sediments of the Chadron indicate a more rapid flow of the streams, while the Brule clays, of much finer material, show that the currents were less strong and that the local lakes and flood plains were of much greater extent. At Scotts Bluff the Chadron is scarcely exposed and the Brule formation is about 500 feet thick, forming the outcropping rock on all sides of the Bluff. These sediments consist chiefly of pinkish to buff-colored clays, with thin-bedded sandstone and limestone strata near the bottom, while near the top are two beds of volcanic ash, separated by about 100 feet of pinkish to buff clays. The volcanic material was probably transported from the Rocky Mountain or Black Hills regions, either by wind or stream action or by both, and deposited in the lakes. In the Scotts Bluff area this fine-grained clay holds its typical character to the top of the formation and does not carry the sandstone strata which are found farther north and characterize the *Protoceras* beds.

AXIAL SKELETON

Skull

THE greatest differences between *Eporeodon socialis* and *Sus scrofa* are found in the skull. The skeletal parts of the Suidæ have remained fairly uniform and their characters very persistent, exclusive of the skull, from the Eocene to the present. Likewise the various genera of the Merycoidodontidæ show a great similarity in their skeletal elements, with the exception of the skulls, where the effects of evolution are chiefly centralized.

The skull of the larger individual, Cat. No. 13119, is not so well preserved as that of the other, Cat. No. 13118, which will be used for descriptive purposes. A cast of the latter skull has been placed on the mount. All of the other skeletal elements described are in the mounted skeleton of the larger animal. The skull of *Eporeodon* is similar in general aspect to that of the oreodonts which have been so accurately described by Leidy, Cope, and Scott.

Lateral view. With the mandible, the lateral surface is rectangular in *Eporeodon* (Fig. 3); in *Sus* (Fig. 4), triangular. The upper contour is nearly straight, whereas in *Sus* there is a gentle slope upward to the supraorbital foramina, from which point the frontoparietal slope is straight and sharply upcurved to the occipital crest. The skull of *Sus* is long with a greatly lengthened facial section, while in *Eporeodon* the skull is a little shorter with the facial segment very much shorter absolutely. The zygomatic arches are stronger and higher than in *Eporeodon;* in both they are flattened from side to side. The zygomatic process of the temporal bone curves sharply upward posteriorly and forms a rounded recurved projection above and anterior to the meatus acusticus externus, similar to that found in *Promerycochœrus*, whereas *Eporeodon* differs materially from this in that the zygomatic process does not trend upward but is nearly straight, terminating posteriorly above the posterior margin of the postglenoid tubercle. The orbits are closed,

but those of *Sus* are open, as in *Protoreodon* and *Agriochœrus*. The orbits of *Eporeodon* are relatively slightly larger, but the position in both is about the same with respect to the line of vision. They are placed very near to the center in proportion to the total skull length in *Eporeodon*, but in *Sus* their position is very much farther back, being approximately two thirds the distance from the prosthion. This difference is due to the greater absolute lengthening of the face in *Sus*. The anterior orbital margin is very thin in *Eporeodon*, due to the deep lacrimal pit (fossa); in *Sus* it is thick and rounded. The lacrimal fossa in the former is deep and circular; in the latter there is no corresponding pit but rather a broad shallow depression, formed in contiguous parts of the lacrimal, malar, and maxillary bones. Neither *Agriochœrus* nor *Protoreodon* possesses a lacrimal fossa. The fossa for the attachment of the ventral oblique muscle of the eyeball is situated just inside of the anteroinferior orbital margin and is much more pronounced in *Sus*. The infraorbital foramen of the latter, relatively a little larger than that of *Eporeodon*, is located above the anterior portion of the fourth premolar; that of the other genus, nearly above the center of the third premolar. The posterior edge of M^3 is almost directly below the temporal process of the malar bone, while that of *Sus* has a position below and only slightly posterior to the anterior border of the orbit. The canine of *Sus* stands about midway between the premaxillary border and the infraorbital foramen. It is directed sharply outward, downward, and then upward and is much flattened. In *Eporeodon* this tooth is located beneath the anterior tip of the ossi nasi, is directed straight downward, and is trihedral in shape with the inner flat side at right angles to the sagittal plane. Owing to the much greater relative size of the premaxilla in *Sus*, the three incisors are plainly visible from the side view, but in *Eporeodon* the third incisors are seen, while the second are very slightly visible and the first not at all. In the latter they increase in size from first to third, while in the former they decrease from first to third. In *Sus* the temporal fossa is entirely

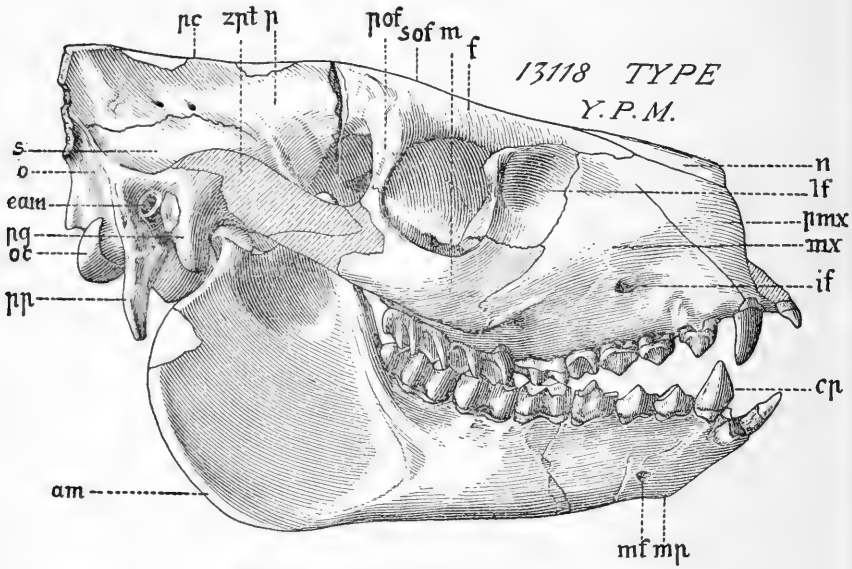


Fig. 3. Lateral view of skull and jaws of *Eporeodon socialis* Marsh. (*am,* angle of mandible; *cp,* Pm_1 or caniniform premolar; *eam,* external auditory meatus; *f,* frontal; *if,* infraorbital foramen; *lf,* lacrimal fossa; *m,* malar or jugal; *mf,* mental foramen; *mp,* mental prominence; *mx,* maxilla; *n,* nasal; *o,* occipital; *oc,* occipital condyle; *p,* parietal; *pc,* parietal crest; *pg,* postglenoid process or tubercle of squamosal; *pmx,* premaxilla; *pof,* postorbital process of frontal; *pp,* paramastoid process; *s,* squamous temporal bone; *sof,* supraorbital foramen; *zpt,* zygomatic process of temporal bone.) Cotype Cat. No. 13118 Y.P.M. ×½.

lateral and its long axis nearly vertical, but in the other genus this fossa is lateral only in the squamous portion of the temporal bone and its long axis is very nearly horizontal. The length of the fossa along its greater axis is, relatively, considerably more than in *Eporeodon.* The postglenoid tubercle in *Sus* is extremely small and unimportant, but in *Eporeodon* it is very large and robust, being 13 mm. in length below the ventral surface of the temporal condyle, while its anteroposterior diameter is 10 mm.

The horizontal ramus of *Sus* is broader and transversely heavier but has a smaller vertical diameter; the angle of the condyle is relatively weaker and does not have the rugosities for

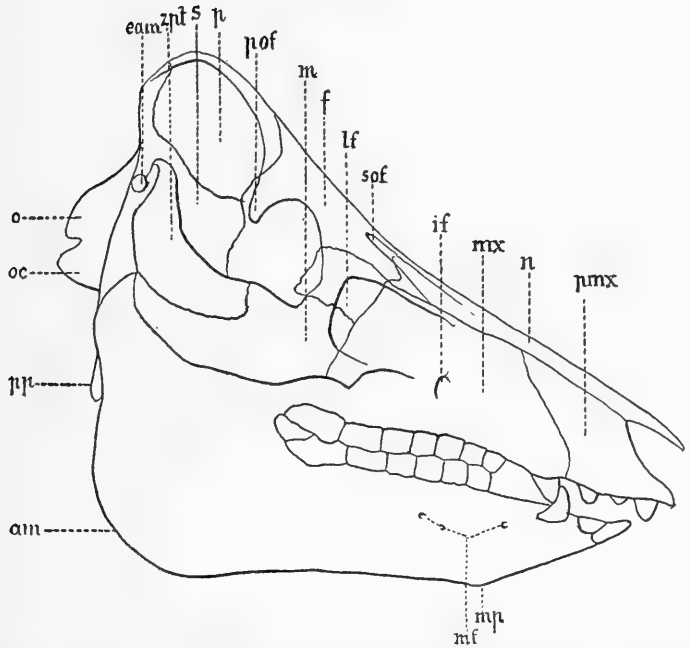


Fig. 4. Outline of lateral view of skull and jaws of *Sus scrofa* Linnæus. (For legend, see Fig. 3.) ×½.

muscle attachment so well developed as in *Eporeodon*. The condyles are ridge shaped, but in *Sus* they are rounded and knob-like. The ascending ramus is broader anteroposteriorly than in *Sus*. The slope of the symphysis is nearly the same in both. The inferior canine (P_1) is vertically triangular and not at all recurved, while that of *Sus* is strongly recurved backward. The incisors are very much heavier and very much more laterally placed than in *Eporeodon*. Their direction is nearly 45 degrees from the alveolus, but those of *Eporeodon* are slightly more nearly vertical. There is a short diastema between the true canine and the first premolar (caniniform premolar) and none between that and P_2, but a relatively large one between the true canine and P_1 in *Sus*. The last three premolars are crowded so that their long diameters are oblique to the line of the mandible. Such is not the case in the other genus.

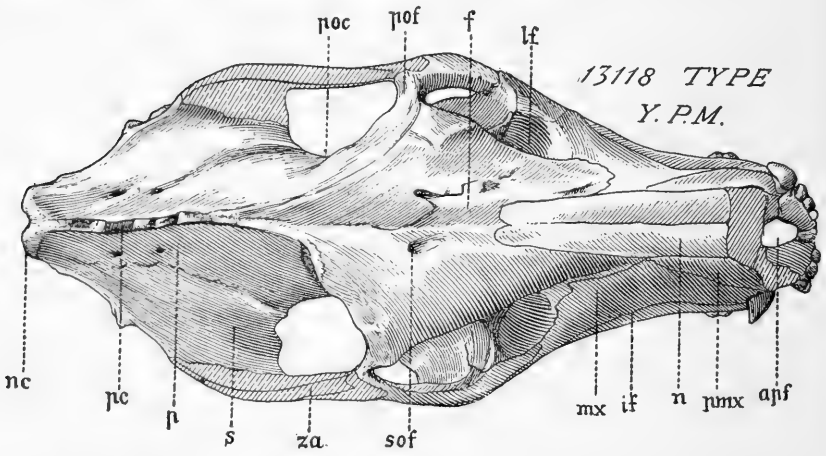


Fig. 5. Superior view of skull of *Eporeodon socialis* Marsh. (*apf,* anterior palatine foramen; *f,* frontal; *if,* infraorbital foramen; *lf,* lacrimal fossa; *mx,* maxilla; *n,* nasal; *nc,* supraoccipital or nuchal crest; *p,* parietal; *pc,* parietal crest; *pmx,* premaxilla; *poc,* postorbital constriction; *pof,* postorbital or supraorbital process of frontal; *s,* squamosal; *sof,* supraorbital foramen; *za,* zygomatic arch. Cotype Cat. No. 13118 Y.P.M. ×½.

Superior view (Figs. 5 and 6A). The most apparent difference between the skulls of *Sus* and *Eporeodon* is that the former has a great lengthening of face. The nasals form a narrow ridge, with a slightly concave crest throughout their entire length. The maxillary bones flare along the alveolar border. In *Eporeodon* the face is filled out so that in cross section it is ovate with the end truncated. The supraorbital foramina in *Sus* are on a transverse line with the anterior rim of the orbits; in the other they are situated nearly on a line drawn transversely through the middle of the orbits. The grooves leading from these foramina in *Sus* are directed slightly inward and forward to the nasals, and then they turn ventrolaterally above the infraorbital foramina; those of *Eporeodon* are less pronounced and follow the same general course, but they vary somewhat in different specimens. In the latter the parietal bones terminate in a medial crest, forming a sharp ridge between the junction of the frontals and the nuchal crest 57 mm.

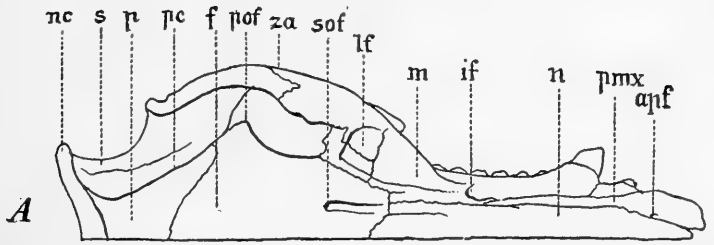


Fig. 6A. Outline of superior view of *Sus scrofa* Linnæus. (For legend, see Fig. 5.) ×½.

long, but in *Sus* the parietal crest, broad and flat, forms the continuation of the frontal ridge from the supraorbital processes of the frontals to the nuchal crest, and the two sides do not meet. The length of the parietal crest, including the frontal crest, is 63 mm. The superior view of the *Sus* cranium shows a nearly equilateral triangle, whose base is a transverse line between the supraorbital processes of the frontals and whose sides are formed by the parietal crests. The apex of the triangle is truncated by the nuchal crest. In *Eporeodon* the cranial area is very differently shaped, being more like that of the White River Felidæ and not at all hog-like. There is no postorbital constriction, or, if any, it is but extremely ill defined, in *Sus*, while in *Eporeodon* it is as well marked as in the Carnivora. The wings of the nuchal crest of *Sus* are approximately 32 degrees from the sagittal plane, and those of *Eporeodon* are about 48 degrees. The zygomata are slightly more outwardly curved in *Sus* than in *Eporeodon*, where they are nearly straight. The glenoid portion of the temporal is considerably heavier than in *Sus*. The lacrimal fossæ produce a marked preorbital constriction not found in the former. The outline of the *Sus* skull, as seen from above anteroposteriorly, is oblongate to the infraorbital foramina, then roughly triangular with the base a little posterior to the temporal condyles, while with the other genus it is triangular to the anterior border of the orbits, then oblong to the temporal condyles, ending in a small triangle whose apex is the nuchal crest. As stated above, the temporal

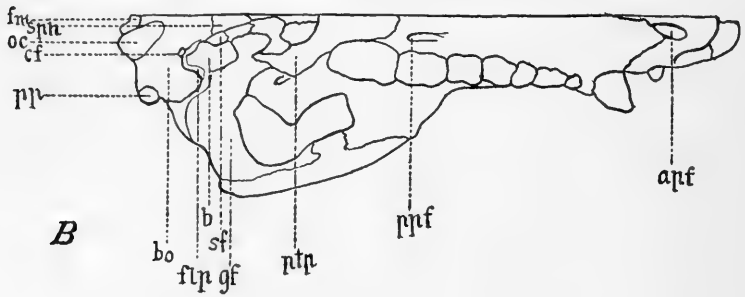


Fig. 6B. Outline of inferior view of *Sus scrofa* Linnæus. (For legend, see Fig. 7.) ×½.

fossa in *Eporeodon* is very much larger than in *Sus*. The canine alveolus is very much heavier and more prominent in *Sus*. The total length of the parietal bone, measured along the sagittal plane, is 44 mm., and in *Eporeodon* it is 69 mm. The premaxillaries are well developed and separate, although in contact in the median line. The other species of the Merycoidodontidæ, except *Agriochœrus*, where the premaxillaries are reduced and not in contact in the median line, either have them separate but in contact or coössified at their tips.

Inferior view (Figs. 6B and 7). The distance from the prosthion to the maxillary-palatine suture, measured along the sagittal plane, is 130 mm., but in *Eporeodon* it is only 92 mm. The tooth rows in both are parallel and about the same distance apart. The molars of both increase in size from first to third. The length of the tooth row from C to M^3 inclusive is 116 mm., and in *Eporeodon* it is 100.5 mm. The pterygoid process of the palatine terminates in a very small knob, and the whole process extends backward and slightly downward, while that of *Sus* turns abruptly downward, ending in a heavy knob (hamular process). The sphenoid bone is quite prominent and extends laterally for 12 mm. in *Sus*, thus being dissimilar to *Eporeodon*. The basicranial axis is nearly parallel to the plane of the palate, but in the latter genus it is directed upward from the basion and obliquely to the plane of the palate. The bullæ are

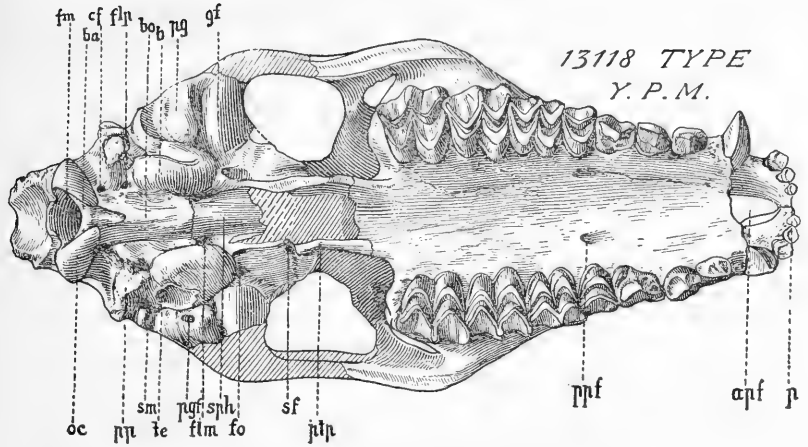


Fig. 7. Inferior view of skull of *Eporeodon socialis* Marsh. (*apf,* anterior palatine foramen; *b,* tympanic bulla; *ba,* basion; *bo,* basioccipital; *cf,* condylar or hypoglossal foramen; *flm,* foramen lacerum medius and anterior opening of carotid canal; *flp,* foramen lacerum posterius; *fm,* foramen magnum; *fo,* foramen ovale; *gf,* glenoid fossa; *oc,* occipital condyle; *p,* prosthion; *pg,* postglenoid process of squamosal or glenoid tubercle; *pgf,* postglenoid fossa; *pp,* paroccipital or paramastoid process; *ppf,* posterior palatine foramen; *ptp,* pterygoid process of palatine; *sf,* sphenoidal fissure or foramen lacerum anterius; *sm,* stylomastoid foramen; *sph,* sphenoid or basisphenoid bone; *te,* point of articulation of tympanohyal element of hyoid arch. Cotype Cat. No. 13118 Y.P.M. ×½.

much inflated, this being the major factor on which Professor Marsh erected the genus *Eporeodon.* These bullæ are oval shaped, occupying the area bounded by the foramen ovale, glenoid tubercle, paramastoid (paroccipital) process, and parts of the basioccipital and basisphenoid bones. The bullæ of *Sus* are triangular in outline with the base set slightly obliquely to the basisphenoid bone. They do not occupy relatively as much area as in *Eporeodon.* The postglenoid tubercles are prominent in this latter, extending 14 mm. below the inferior surface of the temporal condyles. The paroccipital processes are transverse but laterally compressed in their inferior portions. The external auditory meatus is relatively large and situated just anterior to the base of the paroccipital process. In some specimens of *Eporeodon* the anterior portion of the

meatus is expanded to form a wing, but in the cotypes this part is imperfectly preserved.

Foramina. The tympanohyal pit is deep, and the stylomastoid foramen is situated externoposteriorly to it. These foramina are separated by a thin ridge of bone, and the latter is very much smaller than the former. The opening of the stylomastoid is a groove rather than a pit. There is a deep pit for the postglenoid foramen. The condylar foramen and the foramen lacerum posterius are in their normal position. The carotid canal is very small, while the foramen lacerum medius is large and located slightly anterointernally to the bulla. The foramen ovale is small and lies just anterior to the bulla. The foramen lacerum anterius (sphenoidal fissure) is relatively large. Osborn and Wortman first stressed the fact that the foramen rotundum is entirely lacking. *Merycoidodon* possesses this foramen very well developed. In *Eporeodon bullatus* Leidy "the foramen rotundum is represented by two very minute vestigial foraminæ at the sides of the pterygoid plate, between the sphenoidal fissure and the 'foramen ovale.' "[1] The authors further state: "It is more than probable that these will be found wanting in many specimens of this species. In our specimens they certainly could not have been functional, and there can be little doubt that the superior maxillary nerve made its exit through the sphenoidal fissure. The foramen rotundum therefore may be said to be practically absent." *Eporeodon bullatus* is a transitional form, both in its structure and in its stratigraphic position, between *Merycoidodon* and the true *Eporeodon.* The complete loss of the foramen rotundum in the latter indicates a very wide gap in the evolutionary series between this genus and the former, in which this foramen is always present.

Dentition. The formula of the permanent dentition of *Eporeodon* and of *Sus* is $I\frac{3}{3}$, $C\frac{1}{1}$, $P\frac{4}{4}$, $M\frac{3}{3}$, forty-four teeth

[1] Osborn, H F., and Wortman, J. L. Fossil Mammals of the Lower Miocene White River Beds. Collection of 1892. Bull. Am. Mus. Nat. Hist., vol. VI, art. vii, p. 218, 1894.

in all. The apparent fourth lower incisor is about twice the size of the third true incisor and is the true canine with incisiform characteristics. The inferior incisors extend obliquely upward and forward, while the superior ones extend slightly forward and downward, with their crowns pointing wholly downward. The shape of the superior ones is that of an ovoid, convex externally and excavated internally, with sharp edges, while that of the inferior incisors is more like a trapezoid, with nearly flat external outer surfaces and convex inner ones. There is no diastema in the lower mandible between the incisors and true canine and but a slight one between the canine and the caniniform premolar, and none, or only an extremely small one, in the upper jaw between the incisors and canine. The superior canine curves slightly backward and outward, but strongly downward. Its shape is trilateral, sharp pointed, with its sides nearly equal and almost straight. One side is set transversely to the sagittal plane. The inner face has a deep median groove, starting at the base of the crown and gradually dying out downward. The angular interval between the inferior caniniform premolar and true canine received the superior canine. The inferior canine (P_1) is directed forward, outward, and upward. It is placed obliquely in the jaw, strongly convex on its outward face and but slightly convex inwardly. It is laterally compressed, and its edges are acute. The tips are truncated obliquely forward from wear. The crown resembles that of the second premolar, except that the latter is smaller and has an internal ridge. This premolar is also obliquely placed in the jaw. From the position of this functional canine and its close resemblance to the premolar, as well as the presence otherwise of an excess number of incisors, it is without doubt a caniniform premolar and is so considered in this paper. Both upper and lower functional canines are of about the same length but of different shape in each set. The superior canine is separated from the first premolar by a short diastema which received the point of the inferior canine.

There are four premolars above and four below. The upper

ones increase successively in size from first to fourth. The anterior three are of the same pattern—oblong in basal outline, medially divided in an anteroposterior direction by an acute ridge, terminating in an apex. An internal medial transverse ridge joins the apex with the base of the crown. The external face is slightly convex, and the internal is excavated on each side of the median transverse ridge, the posterior excavation being the larger. The posterior transverse diameter is greater than the anterior in all of these three superior premolars. In these same teeth the anterointernal excavation is divided anteriorly by a short ridge connecting the main fore and aft ridge and the cingulum, forming a very small anterior pit above the cingulum. The posterior excavation of the third premolar resembles an additional lobe, similar to the internal lobes of the molars. The fourth premolar consists of two transversely placed crescent-shaped demiconoidal lobes quite similar to the molars, but relatively larger. The outer face is concave, divided by a very slight ridge. A minute diastema exists between the first and second premolars on the right but not on the left.

The lower premolars are of a somewhat different pattern. The second and third are obliquely placed in the mandible, compressed oval shaped, with an anteroposterior acute median ridge terminating in an apex. A median internal ridge connects the apex and cingulum. This ridge is not transverse to the main one, but forms an acute angle posteriorly, surrounding a shallow fossa. The anterior fossa is shallower and larger. The fourth premolar is more oblong shaped, and the internal median ridge is situated nearly at right angles to the anteroposterior one. Its internal border is approximately as high as the main apex, thus forming a deep pit in the posterointernal part of the tooth and a deep concavity on the anterointernal part.

The true molars are three in number. Among recent ruminants they resemble those of the deer more closely and are inserted by fangs only. In both series they increase in size from first to last and consist of four crescent-shaped demiconoidal lobes. The superior molars are nearly square, while the inferior

are slightly greater anteroposteriorly, except M_3, which has an extra posterior lobe, producing a greater length in the anteroposterior diameter over the transverse. The pattern of both series of molars is essentially the same. Anteroexternally the lobes form prominent buttresses, laterally compressed at their outer extremities and expanded near the base of the crown. The line of the lower molars is situated well within the outer portions of the upper.

The teeth of *Sus* are so unlike those of *Eporeodon* in pattern that a comparison would be of no value here, since their structure is so well known. The teeth of *Agriochœrus* also show wide departures from the true selenodont type, resembling those of *Hyopotamus*, except for the absence of the anterior intermediate cusp of the molars.

MEASUREMENTS OF SKULL OF *EPOREODON*

	mm.
Prosthion[1] to basion[2]	188.
Prosthion to occipital condyles	199.
Prosthion to nasion[3]	100.
Prosthion to bregma[4]	153.8
Nasion to bregma	61.5
Basion to bregma	73.
Bicondylar diameter	32.
Bimastoid diameter	60.
Biparamastoid diameter at inferior border of occipital condyles	43.5
Width of occiput above basion	62.
Width of postorbital constriction	32.7
Maximum transverse diameter at postorbital arches	86.7
Maximum transverse diameter of cranium	51.
Maximum transverse diameter at infraorbital foramina	50.
Minimum interorbital breadth	51.

[1] *Prosthion:* The most prominent part on the alveolar border between the two upper median incisors.

[2] *Basion:* The mid-point on the anterior margin of the foramen magnum.

[3] *Nasion:* The highest point on the internasal suture.

[4] *Bregma:* The point at which the sagittal and coronal sutures meet.

	mm.
Anteroposterior diameter of bulla	24.7
Transverse diameter of bulla	15.
Depth of bulla below inferior border of glenoid tubercle	14.2
Depth of paramastoid below inferior border of glenoid tubercle	20.
Maximum diameter across outside of glenoid tubercle	70.6
Anterior palatal breadth between roots of canines	25.
Anterior palatal breadth at first premolar	30.
Posterior palatal breadth at third molar	30.5
Length of superior tooth-row, canine to third molar, inclusive	102.7
Length of superior molar series	49.
Length of superior premolar series	43.5
Palatal length,[5] axial	112.4
Vertical diameter of orbit	29.2
Transverse diameter of orbit	27.9
Length of mandibular ramus	159.5
Length of mandibular symphysis	47.4
Height of coronoid above ramus, vertical	94.5
Height of condyle above ramus, vertical	82.2
Length of inferior tooth-row, canine to third molar, inclusive	99.4
Depth of mandible below center of third molar	38.
Width of ascending ramus posterior to third molar	53.

Superior tooth-row:	*Anteroposterior* mm.	*Transverse* mm.
Incisor 1	3.	3.7
Incisor 2	4.	4.7
Incisor 3	4.5	5.5
Canine	8.	8.5
Premolar 1	10.	7.7
Premolar 2	10.4	8.6
Premolar 3	11.3	10.9
Premolar 4	9.6	13.3
Molar 1	14.5	15.7
Molar 2	18.2	19.
Molar 3	20.1	20.

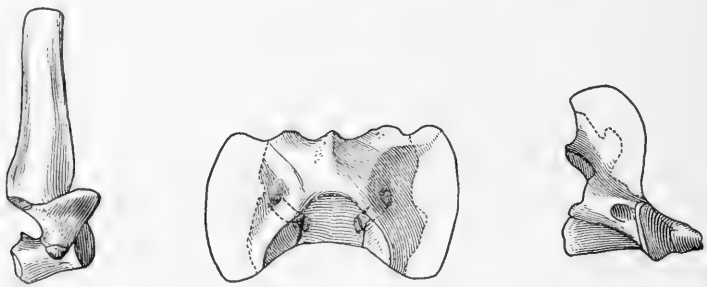
[5] *Palatal length:* Prosthion to posterior surfaces of the maxillary parapets, in axial projection, including the pterygoid processes of the maxillæ, if present.

Inferior tooth-row:	*Anteroposterior* mm.	*Transverse* mm.
Incisor 1	4.	3.2
Incisor 2	4.5	3.3
Incisor 3	4.7	4.
Canine	6.	6.4
Caniniform premolar	11.9	7.2
Premolar 2	12.1	5.7
Premolar 3	13.	7.3
Premolar 4	13.7	9.8
Molar 1	13.7	11.2
Molar 2	17.	13.2
Molar 3	25.2	13.5

Vertebræ

The vertebral formula of *Eporeodon* is C 7, D 13, L 6, S 4, Ca 20+; that of *Sus*, C 7, D 14–15, L 6–7, S 4, Ca 20–23. The cervicals of the former are nearly square and those of the latter, short and wide. The anterior articular surfaces of the centra of both genera are slightly convex and their bodies elliptical in cross section, with the greater diameter transverse. Also in both, the posterior articular surfaces are slightly concave, that is, the vertebræ are opisthocœlous but not markedly so. A well-developed ventral spine is present in *Eporeodon*, with none in *Sus*. The neural canal of the former is nearly circular with a slight convexity of the floor; of the latter it is wide transversely, and the floor is slightly concave. In addition to the foramen transversarium, which is present in both genera, *Sus* has an additional foramen (not found in *Eporeodon*) puncturing the pedicle. The transverse process consists of two branches in both. The small superior branch projects backward and ends in a knobby process, while the ventral branch is an osseous plate extending outward and downward, but in *Eporeodon* this projects downward, outward, and forward, with its free end considerably thickened. The spines increase in size in both from third to last inclusive, but those of *Eporeodon* are relatively a little longer. In the latter all of them project forward, except

the seventh (Fig. 8) which is vertical, but the anterior ones of *Sus* project backward and the posterior, forward. The spine of the last cervical is of great comparative length in *Sus*, but in *Eporeodon* it is but little longer and stouter than that of the sixth. Both do not possess the ventral transverse process, but they do have a pair of small facets on the lateral borders of the posterior articular surface for the heads of the first ribs.



8 9 10

Fig. 8. Seventh cervical vertebra of *Eporeodon socialis* Marsh.
Fig. 9. Atlas of *Eporeodon socialis* Marsh.
Fig. 10. Axis of *Eporeodon socialis* Marsh.
Cotype Cat. No. 13119 Y.P.M. ×½.

The atlas (Fig. 9) is more nearly square from a superior view than that of *Sus*, which has a much greater transverse diameter. The articular cavities for the condyles of the skull are relatively shallow in *Sus*, whereas those of the older genus are deep and large, and the anterosuperior part of the arch overhangs them. The facets for the axis are like those of the deer. The large, round dorsal tuberosity of *Sus* occupies a central position in both diameters, but in *Eporeodon* the tuberosity, which is heavy, terminates in a sharp point located nearly over the anteromedial margin. The alar and intervertebral foramina occupy relatively the same position in both genera. The wings are flattened with a heavy posterior tuberosity. The ventral tubercle of *Eporeodon* is a thick, short, rounded spine, projecting back under the axis, but that in *Sus* is long and laterally compressed. The posterior articular surfaces of *Eporeodon* are larger and the anterior more deeply situated than in the other genus.

Exclusive of the dorsal spine of the axis, the larger diameter of this vertebra is transverse, but in *Eporeodon* it is anteroposterior. The posterior articular surfaces and the dorsal spine are similar in both genera. The anterior articular surfaces of *Sus* stand nearly vertical to the horizontal plane of the centrum, but those of *Eporeodon* are markedly convex, standing at an angle of about 30 degrees from the perpendicular. *Eporeodon* has a well-marked ventral spine which *Sus* lacks. The posterior end of the spine is considerably thickened. The floor of the neural canal is medially divided by a ridge of bone 2.2 mm. high, which is not so in *Sus*. The odontoid process of the axis of *Sus* is a thick cylindrical rod, whereas that of *Eporeodon* (Fig. 10) is oval with the longer diameter transverse. Its shape is therefore quite different from that of *Sus*. The neural canal is oval with the greater diameter vertical, but in the other it is nearly square. The dorsal spine is restored and may be subject to a slight revision. However, I think it was not prolonged so far anteriorly as in *Agriochœrus*, but was rather more like that of *Merycoidodon*.

	Eporeodon mm.	*Sus* mm.
Length of atlas, anteroposterior	40.	39.
Width	55.	67.
Height of dorsal tuberosity	12.4	11.
Width across posterior articular surfaces	33.	41.8
Width across anterior articular surfaces	34.5	51.
Vertical diameter of neural canal	17.	21.
Horizontal diameter of neural canal	16.	21.5
Length of centrum of axis, including odontoid	37.3	37.
Transverse diameter across anterior articular surfaces	30.5	40.5
Transverse diameter across posterior articular surfaces	20.8	30.4
Transverse diameter across odontoid at centrum	15.2	9.7
Vertical diameter across odontoid at centrum	8.3	11.6
Height of posterior articular surface above base of ventral spine	29.	31.4
Vertical height of neural canal	13.	13.
Horizontal diameter of neural canal	7.	15.

The fourth cervical of *Eporeodon* is similar to that of the pig in many ways. It differs in that it possesses a well-defined ventral spine, posteriorly thickened; a much longer dorsal spine in relation to its other dimensions; and a differently shaped neural canal.

	Eporeodon mm.	*Sus* mm.
Length of centrum	23.5	20.6
Width across anterior articular surfaces	26.5	35.
Width across posterior articular surfaces	27.5	34.5
Width of neural canal	11.	17.
Height of neural canal	10.	10.5
Length of dorsal spine	12.	15.

The seventh cervical (Fig. 8) differs but slightly from that of *Sus* except in size. The dorsal spine is heavier and proportionately as long as that of the latter, while the ventral spine has become merely a ridge. The anterior articular surface is convex and nearly circular, while *Sus* has an oval shape. The facets on the lateral borders of the posterior articular surfaces, for the heads of the ribs, in *Sus* are convex and round, while in *Eporeodon* they are ovate with the greater diameter vertical.

	Eporeodon mm.	*Sus* mm.
Length of centrum	21.	19.3
Diameter across anterior articular surfaces	29.5	35.5
Diameter across posterior articular surfaces	26.	29.
Width of neural canal	10.	20.
Height of neural canal	9.	13.5
Length of dorsal spine (first column estimated)	40.	55.

The cervical and first two dorsal vertebræ of Cat. No. 13118 are articulated and bent backward to the most extreme position possible without disarticulation, caused in all probability by ordinary post-mortem desiccation.

The dorsal centra (Fig. 11) in both genera are relatively long and medially constricted. Ventral spines (hypapophyses) are absent on both. The anterior articular processes are more

nearly circular than those of *Sus*, which are elliptical. The posterior articular processes of both are also elliptical and centrally depressed. The arch of *Sus* is perforated by a foramen on each side, but in the other this is not so, because there is no posterior root of the arch enclosing the foramen. In other words, it is an open canal instead of being enclosed by a bridge of bone. There is no foramen in the posterior parts of the roots of the transverse processes. There are metapophyses on all the dorsal vertebræ of *Sus* with the exception of the first two and on all in

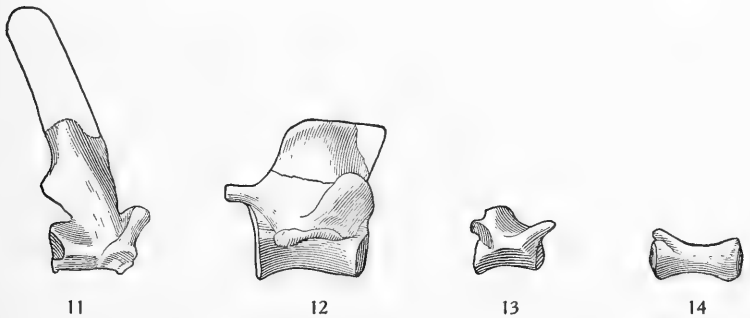


Fig. 11. First dorsal vertebra of *Eporeodon socialis* Marsh.
Fig. 12. Fifth lumbar vertebra of *Eporeodon socialis* Marsh.
Fig. 13. Second caudal vertebra of *Eporeodon socialis* Marsh.
Fig. 14. Thirteenth caudal vertebra of *Eporeadon socialis* Marsh.
Cotype Cat. No. 13119 Y.P.M. ×½.

Eporeodon except the first, and in both genera in the posterior five or six they project from the anterior articular processes. The dorsal spines of both are broad and long. In *Eporeodon* they extend backward to the eleventh vertebra, which may be termed the "anticlinal vertebra" or "center of motion." These spines diminish in size posteriorly to about the eleventh. In *Sus* the first dorsal spine extends slightly forward, the others backward to the tenth, which is the anticlinal, and the posterior vertebræ again project forward. They also decrease in width and length to the tenth, beyond which they are nearly equal in height. The superior edges of the spines are slightly enlarged in both.

	Eporeodon mm.	*Sus* mm.
Length of centrum of first dorsal vertebra	22.	21.5
Width of neural canal	10.	20.
Height of neural canal	11.	11.9
Width of dorsal spine at top of arch	16.5	15.
Height of dorsal spine	63.	85.5
Diameter across anterior articular surfaces	22.	30.

The shape in cross section of the neural canal is slightly more elliptical than round, with the greater diameter vertical, whereas in *Sus* it is also elliptical but with the long diameter horizontal. The anterior articular surfaces are oblong anteroposteriorly, whereas in *Eporeodon* they are slightly oblong, but in a transverse direction.

In the seventh dorsal the shape of the neural canal has changed very markedly, so that it is now horizontally elliptical, but in *Sus* it has become nearly circular. In other respects there is barely any difference between the dorsals in both genera, except that in none in *Eporeodon* is the intervertebral canal posteriorly closed.

	Eporeodon mm.	*Sus* mm.
Horizontal diameter of neural canal in seventh dorsal	10.2	13.
Vertical diameter	6.2	12.

The lumbar vertebræ (Fig. 12) number six in both genera, although *Sus* may have seven. The centra are longer than those of the dorsals and, in the latter, have a well-defined ventral crest which is much less prominent in *Eporeodon*. In *Sus* the centra become progressively flatter and wider in the posterior part. The length of this section of the column is nearly the same in both genera. The notches at the posterior bases of the arches become progressively greater toward the posterior of the series in both, but in *Eporeodon* they are relatively smaller. Superiorly the arches are not so deeply notched as in *Sus*. The metapophyses are better defined than in the latter and extend outward and backward. The transverse processes are nearly equal

in length and width throughout the series, but those in *Sus* increase in length from first to fifth, the latter being comparatively quite small. They do not bend downward in *Eporeodon*, nor do they flare outward at their distal extremities. They do not articulate with the sacrum in either genus. The dorsal spines are thin and broad in both and incline forward, except the last, which is small and vertical in *Sus*. Those of *Eporeodon* are nearly equal in height, which is not true in the other genus. The tongue and groove articulation of the lumbar zygapophyses is well developed, suggestive of that of the creodonts.

	Eporeodon mm.	*Sus* mm.
Height from base of centrum to top of spine of third lumbar	41.5	53.
Diameter across transverse processes	63.	112.
Diameter across posterior articular surfaces	20.4	25.5
Diameter across anterior articular surfaces	28.	33.5
Length of centrum	30.	31.5
Anteroposterior diameter across articular surfaces	38.3	42.
Basal width of dorsal spine	21.	19.4
Height of neural canal	8.	12.
Width of neural canal	10.	15.7

The sacrum consists of four ankylosed vertebræ, to which the first caudal is united in this specimen. The sacrum of *Sus* has also four vertebræ united. The first vertebra and anterior part of the second were joined to the ilia by an articulation and the others to the ischium by very strong ligaments. In both genera the sacrum is but slightly curved. The spines are well developed, gradually diminishing in size, but are still quite broad in the first caudal. In *Sus* the spines are usually absent or but faintly developed. The transverse processes are separate, broad, and plate-like, while in *Sus* they resemble those of the ox, forming a continuous osseous process in an anteroposterior direction. The total length of the ankylosed sacral and first caudal vertebræ is 113 mm.

The number of caudal vertebræ in *Eporeodon* (Figs. 13 and 14) is twenty-one, but there should be at least two more if the

tail tapered as in the pig. The number in *Sus* varies between twenty and twenty-four. Those of *Eporeodon* in the anterior part of the series are short and broad, possessing complete neural arches, well-defined metapophyses, and anterior and posterior zygapophyses. In *Sus* the first four or five caudals have functional articular processes, which become smaller and nonarticular on the succeeding vertebræ. The first ten in *Eporeodon* have well-developed single transverse processes and a neural arch, which gradually diminishes in size to the twelfth, which has no arch. The transverse processes of the first two caudals bend slightly backward; the third and fourth bend forward; and the remainder, up to and including the tenth, again bend backward. Beyond the tenth the transverse process is very much reduced and limited to the posterior extremity of the centrum, while an anterior one appears on that extremity. Including and beyond the twelfth, a pair of processes at each end of the centrum represents the neural arch. Beginning at the anterior end the centra are short, gradually increasing in length to the thirteenth and again diminishing in length to the tip. The posterior vertebræ are cylindrical in shape. It is possible, although there is no evidence upon which to base conclusions, that *Eporeodon* had chevrons, since its European Eocene ally, *Anoplotherium*, appears to have had these bones beneath the vertebræ of its long tail.

	mm.
Length of centrum of third caudal	18.2
Width of centrum, including transverse process	34.
Axial length from anterior to posterior zygapophyses, incl.,	24.
Distance from base of centrum to top of spine	16.
Width across anterior zygapophyses, including metapophyses	19.
Width across posterior zygapophyses	10.
Height of neural canal	4.5
Width of neural canal at top of centrum	6.
Length of centrum of thirteenth caudal (Fig. 14)	24.5
Width across posterior transverse processes	12.3
Vertical diameter from hypapophyses to metapophyses	13.9
Width across metapophyses	5.

Length of centra:

	mm.		mm.
Dorsal 1	22.	Caudal 1	18.7
Dorsal 2	20.5	Caudal 2	19.
Dorsal 3	21.	Caudal 3	19.
Dorsal 4	23.	Caudal 4	18.5
Dorsal 5	24.5	Caudal 5	18.5
Dorsal 6	23.	Caudal 6	19.
Dorsal 7	22.	Caudal 7	19.
Dorsal 8	21.5	Caudal 8	21.
Dorsal 9	21.2	Caudal 9	19.5
Dorsal 10	22.	Caudal 10	20.
Dorsal 11	23.	Caudal 11	23.
Dorsal 12	23.	Caudal 12	24.
Dorsal 13	25.	Caudal 13	25.
		Caudal 14	23.5
		Caudal 15	23.
Lumbar 1	27.	Caudal 16	23.
Lumbar 2	28.	Caudal 17	23.
Lumbar 3	29.	Caudal 18	21.
Lumbar 4	29.	Caudal 19	21.
Lumbar 5	28.	Caudal 20	18.2
Lumbar 6	28.	Caudal 21	16.2

Ribs

There is almost no rib material, these bones having been modeled. The anterior ones are fairly stout and wide, while the middle are large, affording space for a large chest, and the posterior are smaller and rounder. No sternal bones are present, and these were restored from *Sus* in part and may be somewhat revised later.

APPENDICULAR SKELETON

Scapula

THE scapula (Fig. 15) of *Eporeodon* is represented by the distal fourth of three scapulæ, the best preserved of which belongs to Cat. No. 13118 and is used for description. This specimen includes the coracoid, glenoid cavity, acromium, metacromium, and part of the spine. The scapulæ of Cat. No. 13119 have been restored, except the distal parts, after the pattern of *Merycoidodon culbertsonii*. The spine divides the external surface into two subequal fossæ. The acromium projects over the neck and is directed toward the coracoid process. It is transversely distended near the end and terminates in a point. The metacromium is small but distinct, its tip being 22 mm. above the acromium and at the same time being more extended along the crest of the spine. In *Sus* the metacromium is very strongly developed, located near the middle of the spine. In the other artiodactyles it is situated also near the middle of the spine, being represented by only a slight thickening of the crest. The neck is very narrow transversely. The coracoid is well-developed but relatively smaller than in *Sus*. The axillary border is thick with its surface roughened for the attachment of the triceps muscle. The crest of the spine curls over posteriorly at right angles to the main body, while the vertical part of the spine is extremely thin, except at its distal termination. The scapula of *Eporeodon* corresponds closely to that of *Agriochœrus*, except that the greatest diameter of the glenoid

Fig. 15. Scapula of *Eporeodon socialis* Marsh. Cotype Cat. No. 13118 Y.P.M. ×½.

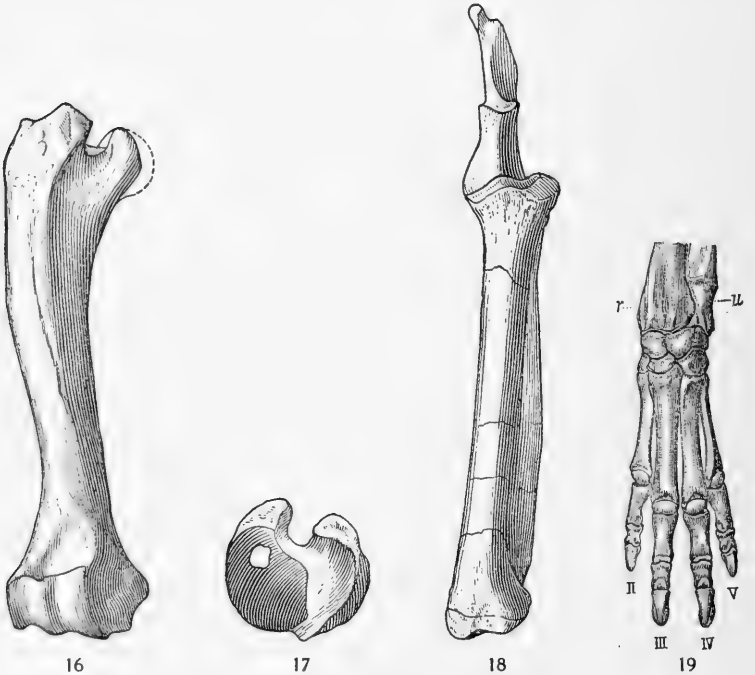
fossa in the former is anteroposterior and in the latter, transverse. In *Sus* the postscapular fossa is much larger than the prescapular; the acromium is far less developed and situated considerably farther back; the metacromium is much more strongly developed and located about medially on the crest of the spine. The position of the acromium and metacromium is very similar in *Eporeodon* to that of recent carnivores in which the acromium extends over the neck and in the direction of the coracoid, while the metacromium is but slightly removed from the acromium and located on the distal end of the spine. The spine of the carnivore scapula divides it also into two subequal parts, as in *Eporeodon* and in *Agriochœrus*.

	Eporeodon mm.	*Sus* mm.
Length, including tuber scapulæ	151.	157.5
Length from anterior to posterior angles	89.5	97.
Width from anterior to posterior borders	77.	76.
Maximum width of neck	20.	20.5
Minimum width of neck	9.	10.
Width, subscapular fossa to tuber spinæ	23.	25.
Length of spine	110.	130.
Length, posterior angle to proximal end of spine	69.	72.5
Length, center of spine to proximal end of spine	104.	65.
Length, center of tuber spinæ to acromium	34.	62.
Width across glenoid and tuber scapulæ	29.	33.
Width across glenoid fossa	20.	22.
Length of suprascapula, long diameter of scapula, estimated	26.	28.8
Length of suprascapula, at right angles to long diameter, estimated	106.	118.

Humerus

The humerus (Fig. 16) is about the same length as that of *Sus*, but it is far less robust. The head (Fig. 17) has nearly the same shape, but does not overhang the shaft as far as in the pig. Again, the external tuberosity is less prominent and does not extend so far above the articular surface as in *Sus*. The medial and lateral tuberosities are well marked in both genera. The

bicipital groove is shallow and undivided. The external and lateral tuberosities are separated by a wide deep groove. The shaft of *Sus* forms a sigmoid curve, while it is nearly straight in *Eporeodon*. Likewise it is compressed transversely near the dis-



16 17 18 19

Fig. 16. Humerus of *Eporeodon socialis* Marsh.
Fig. 17. Head of humerus of *Eporeodon socialis* Marsh.
Fig. 18. Radius and ulna of *Eporeodon socialis* Marsh.
Cotype Cat. No. 13119 Y.P.M. ×½.
Fig. 19. Left manus of *Eporeodon socialis* Marsh. Cotype Cat. No. 13119 Y.P.M. (After Marsh.) ×⅓.

tal end in the former, but the flattening in the latter genus is in an anteroposterior direction. The lateral tuberosity does not rise above the articular surface, as in the pig, sheep, camel, and deer. In this respect it resembles *Agriochœrus* rather than *Merycoidodon*. The shaft of *Eporeodon* is decidedly carnivore-like in appearance, due to its cylindrical form and the anteroposterior flattening at its distal end. Another character not

possessed by the ordinary ungulates is the breadth and unusual size of the internal condyle. The deltoid ridge is weak. There is no entepicondylar foramen. The most dependent part of the bone is formed by the internal flange of the inner trochlea. It is thick and rounded, forming the border of the anconeal fossa. The distal articular surface is divided into an external and internal trochlear surface by a low, thick, rounded carina, located nearer the outer than the inner side, i.e., the articular facet for the ulna much exceeds that for the radius in width. This is true for all of the recent artiodactyles, except that the carina is placed much nearer the outer border than in *Eporeodon*. The external trochlear surface of the latter is much narrower and deeper, terminating externally in a prominent flange. The distal end of this bone resembles more closely in many ways that of a bear than an ungulate. In *Merycoidodon* the two trochlear facets are nearly subequal. The olecranon fossa is very deep and separated from the coronoid fossa by an extremely thin osseous plate. The condyloid ridges are rounded and well defined. The external condyle is quite rugose.

	Eporeodon mm.	*Sus* mm.
Length of left humerus from proximal lateral tubercle to distal end	140.	153.
Diameter of proximal end (maximum)	43.	48.
Diameter of proximal end (minimum)	32.	45.7
Diameter of middle of shaft (minimum)	15.	17.5
Diameter of middle of shaft (maximum)	20.	22.
Diameter across medial lateral condyle	27.	27.
Diameter across medial lateral epicondyle	38.	34.2
Diameter across medial lateral condyle at right angles to above	23.	34.

Radius and Ulna

The radius and ulna (Fig. 18) are approximately the same length in *Sus* and *Eporeodon*. The radius is much more slender in the latter and more curved. It is large at both ends, and the proximal surface extends across the entire humeral trochlear

facet. In *Sus* it gradually increases in size distally, while in the other it abruptly expands near the distal articular surfaces. The proximal articular surface is very suggestive of *Agriochærus*, but probably there was not so much freedom of movement possible as in that genus. The distal end shows no marked peculiarities. The articular facets for the scaphoid and lunare are concavo-convex and much more marked than in *Sus*. Both genera possess a groove on the middle of the front of the distal end; in the latter it is wide and shallow, while in the other it is deep and narrow.

The ulna is long and slender. The olecranon is stout, thick, and oblong shaped in lateral outline. There is a deep groove at its proximal end, probably for the insertion of the tendon of the triceps. In its function and structure the olecranon resembles the patella. The processus anconeus is similar to that of *Sus*. The greater sigmoid cavity is divided by a slight rounded ridge into two nearly equal articular facets. The inferior boundary of this cavity forms a rudimentary coronoid process. The shaft is moderately heavy in its proximal portion, but tapers and flattens medially and distally. There are deep grooves on its outer and inner surfaces. Its distal end shows a distinct articulation for the pisiform. The styloid process is represented by a small rugosity.

	Eporeodon mm.	*Sus* mm.
Length of left radius	117.7	120.
Diameter of proximal end	22.7	24.
Diameter at right angles to proximal end diameter	12.2	16.
Diameter of distal end (maximum)	24.	27.5
Diameter at right angles to next above	15.	21.5
Length from olecranon to distal end of left ulna	157.	160.
Length from olecranon to anconeal process	29.	37.
Minimum diameter at semilunar notch	16.5	20.
Minimum diameter from anconeal process at right angles to shaft	27.	31.
Minimum diameter at proximal junction with radius	19.	17.5

Manus

The carpus of *Eporeodon* is primitive (Fig. 19, reproduced from Professor Marsh's Fig. 162 of "Dinocerata," 1884) for an artiodactyle ungulate. That is, the bones of the carpus are interlocking in that the cuneiform rests upon the unciform, the lunar on the unciform and os magnum, and the scaphoid on the os magnum and trapezoid. In *Agriochœrus* the carpus shows a more serial arrangement in that the cuneiform rests on the unciform, the lunar (semilunar) mainly on the os magnum, and the scaphoid chiefly on the trapezium and trapezoid, with a considerable contact with the os magnum. This is not surprising, because *Agriochœrus* was more specialized in some other respects than the members of the Merycoidodontidæ.

The pisiform bone is well developed, but the trapezium is lacking. The carpal elements are not so flattened as those of *Agriochœrus* and do not differ materially from those of *Merycoidodon* which have been so fully described by Scott. Compared with *Sus* it is seen that the semilunar does not form so distinct a wedge between the os magnum and the trapezoid in that genus. The semilunar (lunar) rests equally upon the os magnum and the trapezoid, and the wrist is more rounded.

The four metacarpals are longer and proportionately slenderer than those of *Merycoidodon* or *Sus*. The pollex has been lost through evolution in both *Eporeodon* and *Sus*. The second and fifth are a little smaller than the third and fourth in the former, but proportionally larger than those of the latter. The proximal end of the third metacarpal does not overlap the head of the fourth to any such extent as in *Sus*. The third and fourth metacarpals possess three phalanges and three sesamoids, while the second and fifth have three phalanges and two sesamoids, in both genera.

The distal ends of the metacarpals and metatarsals are rounded and prominent, that is, they resemble the carnivores rather than the ungulates. A prominent keel is present on the palmar side of the extremity. The slender proximal phalanges

with their expanded heads are also feline in character. The distal articular facets of the median phalanges are carried well back on the dorsal surface, indicating much flexibility of the ungues, which are not so claw-like as in *Agriochœrus*, although they are not the usual primitive artiodactyle hoof found in *Merycoidodon* but seem intermediate in form. They are laterally compressed and curve downward, terminating in a blunt rounded point.

	Eporeodon mm.	*Sus* mm.
Metacarpal II, length, left manus	45.	49.5
Metacarpal II, width at proximal end	9.	4.
Metacarpal III, length	60.	65.
Metacarpal III, width at proximal end	14.	18.
Metacarpal IV, length	55.	64.5
Metacarpal IV, width at proximal end	12.	12.2
Metacarpal V, length	46.	46.
Metacarpal V, width at proximal end	8.7	5.
Phalanx 1, second digit, length	18.	20.
Phalanx 1, third digit, length	21.	32.5
Phalanx 1, fourth digit, length	19.5	32.
Phalanx 1, fifth digit, length	17.	19.
Phalanx 2, second digit, length	9.	10.5
Phalanx 2, third digit, length	12.	21.5
Phalanx 2, fourth digit, length	11.	20.5
Phalanx 2, fifth digit, length	10.	9.
Phalanx 3, second digit, length	9.	12.
Phalanx 3, third digit, length	12.	26.7
Phalanx 3, fourth digit, length	12.	26.7
Phalanx 3, fifth digit, length	9.	11.

Pelvis

No complete os innominatum exists with either of the cotypes, but the ilium and parts of the ischium and pubis, together with the complete acetabulum, were found with both specimens. In restoring the pelvis (Fig. 20), reference was had to the pelvic girdle of two *Eporeodons* from the John Day for-

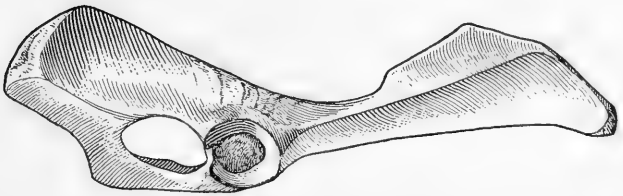


Fig. 20. Os innominatum of *Eporeodon socialis* Marsh. Cotype Cat. No. 13119 Y.P.M. ×½.

mation in this collection which resemble the existing parts of the pelvis of the cotypes. The ilium is longer than the ischium, and in some respects the pelvis is similar to that of *Merycoidodon*. The ilium is widely expanded, possessing a stout tuber coxæ. The transition from the constricted part in advance of the acetabulum to the expanded portion of the ilium is abrupt, as in *Merycoidodon* and the recent suillines, whereas in *Agriochœrus* it is gradual. No trace of the longitudinal ridge, which separates the iliac concavity in the pig, sheep, and deer, is seen in *Eporeodon*. In this respect it resembles the camel, *Agriochœrus*, and *Merycoidodon*. The acetabulum is deeper than in *Sus*, and the cotyloid notch is relatively wider.

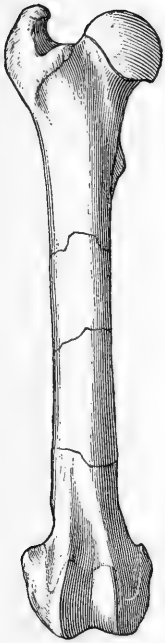
The ischium, as restored, has a considerable vertical depth and passes into the pubis by a rounded border. The inferior and posterior borders are thickened. The ischium above the acetabulum does not show the heavy rugose ridges shown in the pig. The trihedral-shaped posterior termination present in the pig probably does not exist in *Eporeodon*, although in nearly all other respects it is closer to the pig than to that of the other artiodactyles. The pubis is short and stout, much like that of *Merycoidodon*. The obturator foramen is relatively smaller than in *Sus*. The pubic symphysis is relatively longer than in the latter.

	Eporeodon mm.	*Sus* mm.
Length of sacrum	91.25	92.6
Length of centrum of sacral 1	24.	27.
Length of centrum of sacral 2	20.5	21.

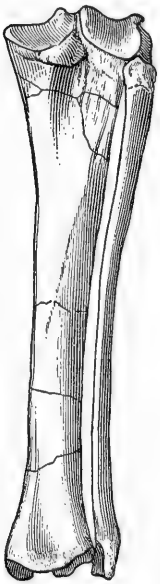
	Eporeodon mm.	*Sus* mm.
Length of centrum of sacral 3	22.	21.5
Length of centrum of sacral 4	22.7	22.
Width of sacral 1, including transverse process	64.	68.4
Width of sacral 2, including transverse process	38.	40.
Width of sacral 3, including transverse process	35.	27.
Width of sacral 4, including transverse process	38.	26.
Width across articular surfaces of sacral 1	34.	42.
Height, inferior edge of centrum to top of spine, sacral 1	27.	20.9
Height, inferior edge of centrum to top of spine, sacral 2	21.5	14.4
Height, inferior edge of centrum to top of spine, sacral 3	20.4	13.
Height, inferior edge of centrum to top of spine, sacral 4	19.	12.7

Femur

The head of the femur is hemispherical and more exserted from the neck than that of any recent ungulate. The oval depression for the attachment of the ligamentum teres is well defined. The neck is elongate and constricted, and the great trochanter rises about as high as the proximal end of the articular surface. There is no third trochanter. In fact, these features resemble those of the carnivore more than of the ungulate type of femur. The digital fossa is deep, which presupposes a relatively large obturator externus muscle. The lesser trochanter, situated slightly on the preaxial side, is conical and relatively rugose. The intertrochanteric lines are rather indistinct, as well as the linea quadrati. The shaft (Fig. 21) is almost straight and nearly circular in cross section. The linea aspera are faintly indicated. The distal end has a considerable anteroposterior diameter. The outer tuberosity is much more prominent than the inner. The internal condyle is the larger and is more rounded than the external. Its articular facet is transversely convex. The articular surface of the external condyle is



21



22

23

Fig. 21. Femur of *Eporeodon socialis* Marsh.
Fig. 22. Tibia and fibula of *Eporeodon socialis* Marsh.
Cotype Cat. No. 13119 Y.P.M. ×½.
Fig. 23. Left pes of *Eporeodon socialis* Marsh. Cotype Cat. No. 13119 Y.P.M. (After Marsh.) ×⅓.

inclined toward the median line, and the intercondyloid notch is deep. Anteriorly the condyles are continuous with each other, forming a concave depression or trochlea for the patella, which is shield shaped, flattened on top and on its posterior side, and convex anteriorly.

Tibia and Fibula

The fibula (Fig. 22) is missing, except for its distal end. The shaft is restored and extended the entire length of the tibia, from which it is separated by a narrow interosseous space. The

external malleolus is larger and wider than the internal and articulates with the astragalus by a triangular facet. It is externally deeply grooved for the tendons of the peroneus longus and brevis muscles. Its edge is very rugose, affording attachment to the external lateral ligament of the ankle joint.

The tibia is similar to that of the artiodactyle type, although somewhat suggestive of that of *Canis*. The spine is prominent and bifid, affording attachment to the semilunar fibro-cartilages and, by clearly marked depressions in front and behind its base, to the crucial ligaments of the joint. The shaft has three sharp ridges. The internal malleolus projects downward below the external, and it is of peculiar shape, being long, stout, and somewhat hook shaped. This hook is received in a deep depression in the astragalus. It has well-marked grooves for the tendons of the tibialis posticus and flexor longus digitorum muscles and also affords attachment to the internal lateral ligaments.

	Eporeodon mm.	*Sus* mm.
Maximum length of pelvis	161.5	182.
Length from tuber coxæ to tuber sacrale	57.2	78.5
Minimum vertical diameter of ilium	17.	18.2
Anteroposterior diameter of acetabulum	22.3	26.
Transverse diameter of acetabulum	21.4	26.2
Minimum horizontal diameter of pubis (acetabular)	14.4	10.
Minimum vertical diameter of pubis (acetabular)	6.3	6.
Length of pubic suture	44.2	52.7
Maximum width across acetabuli	80.8	96.
Maximum width across posterior end	96.	94.
Length of left femur from head to medial condyle	168.	171.
Maximum diameter across proximal end	40.	44.
Mimimum diameter across proximal end	23.	28.
Maximum diameter across head	21.5	22.
Maximum diameter across distal end	41.5	47.
Maximum diameter across distal end at right angles to first above	35.	37.

	Eporeodon mm.	*Sus* mm.
Maximum diameter across center of shaft	17.	25.
Minimum diameter across center of shaft	14.5	16.
Width of left patella	20.	16.
Length	21.2	30.
Maximum thickness	14.5	16.
Length of left tibia from spine to distal end	153.	161.
Maximum diameter across proximal end	38.	38.
Minimum diameter across proximal end	26.5	30.
Minimum diameter across center of shaft	14.	17.
Maximum diameter across center of shaft	15.	18.5
Maximum diameter across distal end	24.	26.2
Minimum diameter across distal end	19.	21.5
Length of left fibula	141.	144.
Diameter of head at distal end	12.5	14.
Thickness of head at distal end	5.	6.

Pes

The tarsus of *Eporeodon* resembles that of the pig (Fig. 23, reproduced from Professor Marsh's Fig. 163 of "Dinocerata," 1884), although the astragalus is heavier and wider. The trochlear surface comprises two unequal articular facets, divided by a deep, strongly convex groove. The external condyle is much the longer, terminated anteriorly by a deep fossa, separating it from the cuboidal facet below. The fossa is much deeper than that in *Sus*. The inner condyle is much smaller with a sharper crest, due to the lateral articulation for the internal malleolus. The distal extremity of the astragalus is divided into two articular facets, one for the navicular being deeply concave transversely, and the other for the cuboid being convex longitudinally and straight transversely with a slight pitch toward the calcaneum. In the pig, *Merycoidodon*, and *Eporeodon* the facet for the cuboid is extended around onto the posterior surface. The calcaneum resembles that of *Sus* in all essential details. The groove for the tendon of the plantaris muscle is well shown on the inner side of the tuber calcis. The

tuber is about equally developed in both genera. The osseous ridge for the attachment of the external lateral ligament is quite prominent and situated a little below and to the side of the articulation for the external malleolus.

The cuboid is relatively similar in both genera and not depressed, as in *Agriochœrus*. Its superior surface bears the two facets for articulation with the calcaneum and astragalus, the former being flat and inclined forward, and the other quite concave. The navicular is deeply concave dorsally to receive the astragalus, and it is not flattened, as in the perissodactyles. Its distal surface is flat for articulation with the ecto and mesocuneiform bones, which are relatively the same as in *Sus*. The posterior hook of the navicular overhangs the ecto and mesocuneiform bones and is apparently a distinct character of the artiodactyles, but it is absent in the perissodactyles.

The fourth and fifth metatarsals articulate with the cuboid, and the facets are fairly broad and flat. The two median metatarsals, as well as the second and fifth, are about equal in length and size. Again the carnivore character appears in the large rounded distal ends of the metatarsals. It would seem from the characters of these bones of the manus and pes that the members of this genus were digitigrade, although perhaps unguligrade approaching digitigradism. It is probable that the main flexure of the foot took place at the distal ends of the metatarsals, as in *Chalicotherium*, an undoubted digitigrade type. Distal keels are present on the ventral surface.

The phalanges apparently formed a gentle curve when seen from the side, as in *Agriochœrus*. The proximal articular facets of the proximal phalanges looked forward and upward, which would indicate that the metatarsals were raised from the ground. The median phalanges are shorter but only slightly narrower than the proximal ones. The ungues are much like those of the manus and seem to be intermediate betwen those of *Agriochœrus* and *Merycoidodon*. The hallux has been lost through evolution.

	Eporeodon mm.	*Sus* mm.
Length of left calcaneum	57.5	60.
Width of left calcaneum	12.	15.
Maximum thickness of left calcaneum	8.5	9.
Length of left astragalus	30.	36.
Width of left astragalus	18.5	20.
Average thickness of left astragalus	15.5	19.
Width of left navicular	14.5	11.
Length of left navicular	18.	22.5
Height of left navicular	11.5	15.
Width of left ectocuneiform	14.	
Length of left ectocuneiform	12.	
Height of left ectocuneiform	7.5	
Width of left cuboid	14.	15.
Length of left cuboid	20.	20.
Height of left cuboid	21.	25.
Left metatarsal 2, length	51.	52.
Left metatarsal 3, length	61.5	70.5
Left metatarsal 4, length	60.5	71.5
Left metatarsal 5, length	48.	
Left metatarsal 2, width at proximal end	5.	5.
Left metatarsal 3, width at proximal end	7.	14.5
Left metatarsal 4, width at proximal end	6.	13.
Left metatarsal 5, width at proximal end	4.5	
Left phalanx 1, second digit, length	20.2	19.
Left phalanx 1, third digit, length	24.	29.5
Left phalanx 1, fourth digit, length	24.	30.
Left phalanx 1, fifth digit, length	19.5	
Left phalanx 2, second digit, length	10.2	
Left phalanx 2, third digit, length	13.5	
Left phalanx 2, fourth digit, length	14.	
Left phalanx 2, fifth digit, length	10.	
Left phalanx 3, second digit, length	12.	
Left phalanx 3, third digit, length	15.	
Left phalanx 3, fourth digit, length	14.5	
Left phalanx 3, fifth digit, length	12.	

Additional Copies
of this Bulletin may be procured from
Peabody Museum of Natural History, Yale University,
New Haven, Conn.,
at
30 cents per copy.